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The Mechanical Genesis of the Form of the Fowl's Egg.

By John A. Ryder.

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The configuration of the outline of the hen's egg is determined apparently by mechanical means while the egg-membranes and shell are in process of formation within the oviduct.

The conditions, after the passage of the ovum or yolk proper into the oviduct, seem to be about as follows:

1. In the upper part of the oviduct the albumen is laid down upon the yolk by the activity of the albumen-secreting structures forming the wall of the duct. This albumen is laid down in successive layers, as is proved by the structure of the albumen and chalazæ, when these are coagulated by heat and then cut into thin sections. This lamination of the albumen is a result of the mechanical relations that the yolk sustains to the surrounding albumen-secreting surfaces, and this structure of the albumen is mechanically caused. The chalazæ are produced as the first deposits of albumen in the oviduct behind and in advance of the yolk. The twisting of the chalazæ is mechanically caused for the reason that the twist of the chalaza

at opposite poles of the yolk is in opposite directions. This could not occur except under conditions of rotation of the yolk or true egg during the early steps of its passage down the oviduct. The laminæ of the chalazæ are in a continuous spiral scroll such as is developed by a thin lamina rolled upon itself, such as a scroll of paper. This would seem to prove that a rotation of the forming egg was necessary in order to give rise to the phenomena described.

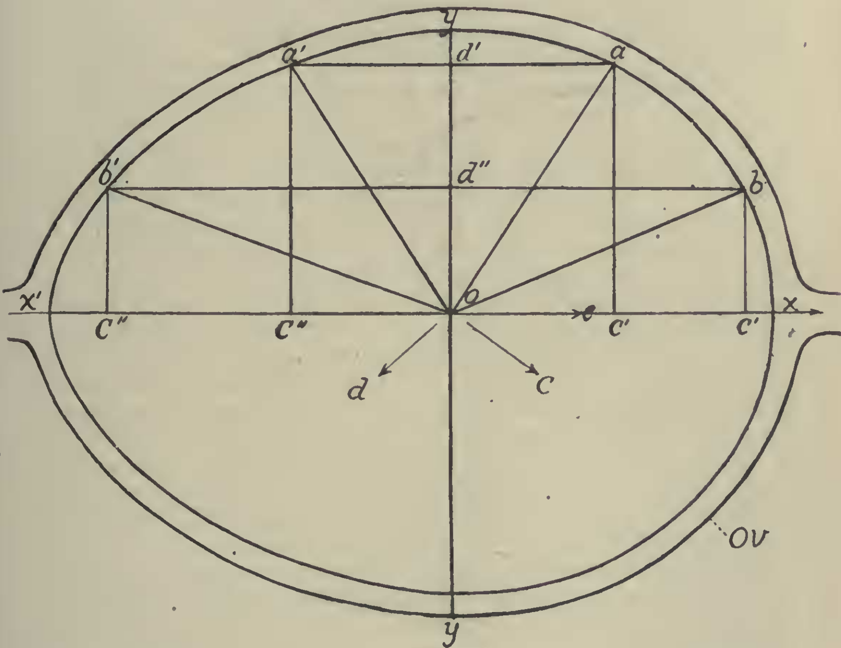
2. The membrana putaminis is deposited in the lower portion of the oviduct. Its fibres are cemented together where they cross one another, showing that they must be formed in a plastic condition. The putaminis, moreover, is laminated, showing that, like the yolk, it is a secretion, the laminæ of which are deposited in succession. It finally covers the entire egg and albumen as a secondary egg envelope, and possesses certain characteristic traits of figure, firmness and elasticity.

3. From the beginning of the process of the development of the secondary egg envelopes in the oviduct there is circular constraint around the yolk and albumen owing to the tubular shape of the oviduct itself. The walls of the latter press upon the contained egg somewhat after the manner of a broad elastic girdle. This pressure around the egg elongates the whole mass in the direction of the long axis of the oviduct. If this pressure of the elastic walls of the oviduct were not associated with peristalsis of the oviduct, in other words, were the forming egg to remain at rest within the duct, it would be deformed only from a spherical to an elliptical figure. This restraint is least at the ends of the mass where it tends to be extended into the lumen of the duct. This elastic annular compression of the forming egg within the oviduct may be regarded as the true cause of the deformation of the hen's egg towards a stable elliptical configuration, while still in the plastic state.

4. After the completion of the membrana putaminis a third homogeneous layer is deposited upon the latter in which the shell is formed. This shelly deposit consists at first of isolated circular nodules of calcareous matter, that only become fused together at a late stage of their deposition ; when in fact they commence to become crowded against one another and pressed into close contact as they enlarge from within outward. Previous to this fusion the shell is flexible, if an egg is prematurely laid with an imperfect shell, as every farmer's boy knows. After the fusion of these minute calcareous plates the shell becomes rigid, as seen in a fully matured egg. It is probable that a certain differential of pressure has been maintained at opposite ends of the egg during the formation of the membrana putaminis, the matrix of the shell, and the shell itself that is instrumental in giving to the hen's egg and birds' eggs in general their particular forms. This differential of pressure at opposite sides of the elastic girdle formed round the egg by the oviduct is caused by the physiological necessity of propelling the egg down the oviduct, or, in other words, is due to the fact that the egg is moved along by forces developed within the wall of the oviduct itself. As this differential of pressure increases on one of the sides of the oviducal

girdle round the egg will the form of the latter depart more and more widely from the figure of a true ellipse and become more and more ovoidal or egg-shaped.

The problem of the development of the figure of the hen's egg is one that may be very easily dealt with mathematically. In fact, judging from the great variety of variations of form presented by eggs it is probable that a different equation would be required for every case, thus showing that the forces operative in the process were themselves variable, a result which is *a priori* most probable. The pressure preventing the passage of the elliptical mass down through an elastic tube must be developed



largely in the form of friction, and the resistance of the walls of the oviduct to dilation. To overcome this a greater pressure must be exerted on the elliptical egg-mass at a point above its minor axis thanbelow the latter. This will tend to squeeze part of its substance, since it is at last enclosed in an elastic capsule before shell formation takes place, into the lower or larger end of the mass. In this way the ovoidal form of the egg seems to have first arisen. The mechanism by which this is accomplished can, however, be best understood by means of a diagram showing the manner and conditions under which the forces involved coöperate.

If the wall of the oviduct *Ov* is supposed to conform to the shape of the egg and to be closed in front and behind it, in a longitudinal section of the egg in place in the oviduct, we should obtain a diagram* somewhat like the foregoing. The major axis of the egg coincides with x, which produced is also coincident with the closed lumen of the oviduct. The minor axis y is transverse to the oviduct. If it is sought to move the egg within the oviduct, dilated as it is, at the point where the egg lies, a certain propulsive force must be developed annularly by the circular fibres in the wall of the duct. This requires that the force exerted from x' to y shall be greater than that exerted from x to y, else the egg will not be moved along x in the direction of e. This implies that the annular muscular coat in the wall of the oviduct shall contract with greater energy from x' to y than from x to y, but as a matter of fact the egg is not elliptical so that the major axis x is cut into unequal parts, $x'\ o$ and $o\ x$ by the axis y. Since this true, if the annular muscular coat of *Ov* be of the same thickness throughout its length by the very conditions which now obtain in respect of the statical equilibrium of the figure of the egg, it would, upon the simultaneous contraction of those parts of the wall of the oviduct in contact with it, be impelled down the latter, or in the direction of e. We stated above, however, that so long as the egg contents were not confined to a rigid envelope and were at rest within the duct that the figure of equilibrium would be an elliptical one through the long axis x of the mass. Now this is just what does not happen and we can only seek the cause for such a departure from the elliptical figure in the added propelling force which must be applied at one side of y in order that the mass may be moved at all. If the fluid mass is not rigid the very application of the greater force on one side of y will cause the elliptical figure of the longitudinal section of the mass at rest to pass into an ovoidal one the instant the mass is put into motion. This simple statement of the facts as to the conditions which obtain will make it self-evident that the force which causes an egg to become ovoidal within the oviduct is developed as a differential of force manifested between two immediately adjacent annular segments of the duct and on opposite sides of y.

The geometrical demonstration of this fact is so simple that it will present no difficulty to any one familiar with the rules of elementary geometry. If two lines $a'\ a$ and $b'\ b$ be drawn parallel to x through y, so as to touch at either end the outline of the semicircumference of the egg and ordinates be then erected, as $a\ c'$ and $b\ c'$ and $a'\ c''$ and $b'\ c''$, four rectangles will be formed which will completely exhibit the quantitative antagonism of the forces developed symmetrically upon either side of y or of x. The two rectangles, $a'\ d'\ c''\ o$ and $b'\ d''\ c''\ o$ are greater in area than the rectangles $a\ d'\ c'\ o$ and $b\ d''\ c'\ o$ on the other side of y. The sum of the diagonals $a'\ o$ and $b'\ o$ of the first pair to the left is greater than that of $a\ o$ and $b\ o$ of the second pair to the right of y, therefore the sum of the former as representing the propelling energy developed by the pressure

*This diagram has been constructed from the outline of a hen's egg very carefully plotted. It therefore represents an actual contour.

of the oviduct from x' to y must be greater than the sum of the first pair representing the resistance developed by the walls of the oviduct from y to x. It is this difference of annular pressure thus developed between x' and y along the curve and y and x along the remainder of the same curve that is responsible not only for the energy which propels the egg along the oviduct, but which also deforms it while in a plastic condition, before rigid membranes are deposited over it, and causes it to permanently assume the ovoidal figure so familiar to every one in the form of the hen's egg.

Pursuing the analysis further, the composition of forces developed from x' to y would take the direction c. Those from y to x would take the direction d. A similar set would be developed from the two inferior quadrants below x, but these we may neglect, since they are of the same value exactly as the pair of antagonistic energies already considered and developed above the axis x. Since $c > d$ the tendency will be for the mass to be propelled in the direction of e and there will thus be a second composition of antagonistic forces in the direction of e which will not only propel the egg along the oviduct, but also tend to deform the egg-mass prior to its becoming encased in a rigid egg-shell.

The development of the figure of the eggs of birds is therefore in all probability a purely dynamical problem or one in which energy is applied in a definite manner to the plastic surface of a mass in statical equilibrium within the oviduct. The moment motion is set up to propel the egg through the duct the forces operative in determining the figure of the as yet unformed shell depend upon the physiological activity and condition of tone of the muscular walls of the oviduct which must first deposit the membrana putaminis, the figure of which as a somewhat elastic closed membrane is determined as here supposed. This in turn definitely determines the figure of the shell, which is deposited upon it. In this way it can be shown that the interplay of energies developed by the soft parts or oviduct have determined the conformation of a hard part or of the shell.

The shell itself is, however, deposited by a process involving the development of a statical equilibrium which is finally satisfied when the development of the shell has been completed. What is meant here is that the shell-matrix is a non-cellular colloidal body which has a strong attraction for soluble, inert, earthy substances such as lime salts, circulating in the fluids of the body. These being particularly abundant, partly as excreta, in the vicinity of the cloaca, near which the shell of the eggs of birds is formed, the source of the supply of these matters is not far to seek. These soluble but inert salts are attracted by this colloidal matrix which they finally saturate when the shell may be said to be completed.

The shell of the eggs of birds has therefore probably been developed statogenetically, while the figure of the shell has been developed kinetogenetically. Both factors are, however, ergogenetic, that is, form and structure has here been developed by the expenditure of energy.

That there has been great variation in the mode of exhibition of the kinetogenetic factor in the development of the shells of eggs is proved by the fact that the latter vary in form very widely. So much is this the case that a distinctly different algebraic formula would have to be worked out for every variation of the form and size of eggs laid by even the same bird. If the very slight disturbances of the counterpoise of the energies on either side of the axis y which condition and determine the figure of such a body as a hen's egg are sufficient to produce the remarkable variations which we may see by the thousand in any marketplace, how slight must be the disturbances of the interplay of the living energies that need to be set up in living bodies in order to produce the endless number of variations that they present. If the figure of the hen's egg is dependent upon the mode and condition of the equilibration of forces developed within an oviduct, what reason is there to doubt that plastic organisms are so modified, only in ways a thousand times more complex and difficult to unravel and explain.

The application of the principle here developed is very extensive. It applies also to an explanation of the oval and ovoidal forms of the eggs of many animals that are manifestly due to causes operating in much the same way. Those of many insects at once occur as a case in point. The elongated blastocysts of mammals growing under a condition of annular constraint within a tubular uterus or uterine tubule are other cases that illustrate the same doctrine. The foregoing discussion also clearly explains why it is that the blunt end of the hen's egg comes down the oviduct as its foremost portion and not the sharp end, as one would be led to suppose, were it not positively established that such is not the case.* It also makes it evident that variations in the figure of the eggs of birds are due to the exhibition of varying quantities of energy and to different conditions of activity of the walls of the oviduct during the formation of the secondary egg envelopes, in the thus protracted process of oviposition.

One may be further permitted to surmise that in its nearly completed state in the oviduct that the prolonged and at first voluntary retention of the egg in the latter by the parent distinctly tended to cause the deposit of the third and last homogeneous matrix into which calcareous infiltration occurred automatically as suggested above. The retention of the egg in the oviduct caused it to act as an irritant when a second and last basement membrane, the matrix of the future shell, was thrown down in the oviduct comparable to that of the basement membrane or zona deposited around the ovum as the vitelline membrane in the ovarian follicle. The evolution of the eggshell itself may, therefore, with the utmost show of probability, be traced to a voluntary and more or less intelligent desire of the female parent to protect its potential offspring for a time within her own body. In carrying out this protective instinct which preceded the habit of nest-building, concealment or burial of the whole laying was resorted to, as still practiced by reptiles, such as alligators and turtles. The entire brood or nestful were also at first laid at once and concealed, and a

* The evidence for this was first adduced by Nathusius, *Zoolog. Anzeiger*, Vol. viii.

crude egg-burrow only, without subsequent parental care, as in the case of Pityophis, was constructed. We can thus understand that the often elaborate and intelligent nest-building habits of Aves were preceded by the far cruder and hastier and simpler nesting habits of the Reptilia, which, on account of the phylogenetic relations between the two groups, should, on *a priori* grounds, be the case.

The origin of the egg-shell of the eggs of birds and reptiles may therefore be traced to physiological causes acting automatically under the control of those instincts or intelligent efforts at self-preservation and protection extended by the parent to the young even while still in the form of the outwardly and apparently quiescent condition of the egg. The prolonged retention of the eggs in the oviducts must have begun in reptiles where the whole laying of a season is found to occupy the oviducts at one time. Such prolonged retention would distinctly tend to develop a shell owing to the operation of agencies that we can in a great measure trace and specify as above. Such a retention of the ova within the oviduct for a period would also distinctly tend to develop the amniote placental and viviparous forms of development, provided the retention of the eggs was from any cause prolonged. There is, in fact, much evidence to indicate that eggshells or secondary egg envelopes were, in the first place, evolved because of the prolonged retention of the eggs within the oviduct by the wary female for purposes of protection. Such a prolonged retention of the eggs in the oviduct was only the prelude to the evolution of placental viviparity and to the highest forms of parental care as exemplified in the human species. Both processes were, therefore, adaptive as they were also manifestly superposed in the order of their development. The mechanical genesis of the amnion was begun in fishes, and was completed amongst higher forms. Its conditions have been in part traced by the present writer and Dr. T. W. Shore. In the same way the successive steps of the evolution of the allantois may be traced. It may accordingly be shown that the lines of demarcation between egg-laying and viviparous vertebrates are in large measure arbitrary, and that if the evolution of these processes be carefully studied, direct and obvious connections can be established between both. Not only is this the fact, but there also now exist sufficient data to establish upon a tolerably firm foundation the doctrine that the various types of placentation are developed as the results of direct mechanical and physiological adaptation. The evidence for this appears quite as clear as that which has been adduced above in regard to the dynamical method and mechanical conditions under which the form of the eggshell is determined in the oviduct of birds.